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DEFENSE OF RIPE FRUIT FROM PESTS: ITS SIGNIFICANCE IN RELATION TO PLANT-DISPERSER INTERACTIONS

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> The world is not green. It is colored lectin, tannin, cyanide, caffeine, aflatoxin, and canavanine [Janzen (1977*a*)].

Many plants depend on vertebrates for the dispersal of their seeds (Ridley 1930; van der Pijl 1972). Fruits, discrete packages containing some seeds plus a certain amount of nutritive material, have originated as a means of dispersing seeds through the provision of attractive food to dispersal agents (Snow 1971; van der Pijl 1972; McKey 1975). Dispersal agents usually ingest the accessory nutritious tissue along with the seeds, obtain a reward as a result of digesting it, and take the seeds away from the parent plant to be later discarded in conditions suitable for germination. Fruit features (color, size, nutrient content of flesh), fruiting patterns (crop size, ripening rates, phenology), and some aspects of frugivore behavior and physiology apparently have been shaped over evolutionary time by means of reciprocal interactions between plants and dispersal agents (e.g., Snow 1965, 1971, 1973; McKey 1975; Walsberg 1975; Howe and Estabrook 1977; Howe 1979; Howe and Vande Kerckhove 1979; Thompson and Willson 1979; Stiles 1980; Herrera 1981*c*, 1982). In particular, natural selection appears to have strongly favored plant features improving the survival of seeds and seedlings (e.g., Janzen 1970; Snow 1971; McKey 1975; McDiarmid et al. 1977; Howe and Primack 1975; Howe 1977; Herrera and Jordano 1981). This implies, among other things, the evolution of traits that "select" the best dispersal agents and decrease the incidence of detrimental organisms damaging the seeds or placing them in unsuitable germination sites.

Once a fruit becomes ripe, it advertises its condition to potential legitimate dispersers by changes in color, texture, taste, conspicuousness, and/or odor. Nevertheless, some time normally elapses between the ripening of a fruit and the moment in which it is found and ingested by an appropriate disperser. The duration of this interval varies in relation to species and, probably, habitat type, and may range from a few hours to many months (e.g., Sherburne 1972; Howe 1977; Morrison 1978; Johnson and Landers 1978; Jordano 1979; Thompson and Willson 1979). During this critical period the fruit is exposed to dispersers, but also to a variety of damaging agents including fungi, bacteria, phytophagous inver-

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tebrates and destructive vertebrates. Ripe fruits are self-advertising structures which contain a nutritive flesh and are found clumped in most instances, thus they probably represent potential food items for most living organisms, not just for dispersers. Most likely, plants not only must attract legitimate dispersers that place undamaged seeds in safe germination sites, but also must actively avoid irreparable fruit or seed damage by other organisms (Howe 1977; Janzen 1977*a*).

Plant traits directed to select the most appropriate dispersers among the set of potential vertebrates in a habitat have been discussed often in the literature (e.g., Snow 1971; McKey 1975; Howe and Estabrook 1977; Howe 1977, 1979, 1980). Nevertheless, the possible adaptations evolved by plants to defend their ripe fruits from pathogens and invertebrates and the potential implications of these adaptations to both plants and dispersers, remain virtually unexplored. Here I will show that: (1) Defense of ripe fruits from pests actually takes place through a variety of mechanisms and often involves the presence of secondary compounds. (2) Toxic fruits may be fairly common in some regional vertebrate-dispersed floras. (3) Chemical defenses in fruits actually represent some competitive disadvantage to plants. (4) Undesirable fruit defense methods may be interpreted as the indirect result of plant competition for the services of dispersal agents. (5) Under some circumstances, chemical defenses may be compatible with the dispersal function of fruits and, in these cases, probably increase the potential for plant coexistence.

DAMAGE TO RIPE FRUITS BY NONVERTEBRATE AGENTS

Published records of injury to wild ripe fruits suggest that predispersal damage frequently occurs. Phalangids (Thompson and Willson 1978), drosophilid flies (Rust and Roth 1981), beetles (Della-Bianca 1979; Rust and Roth 1981), lepidopterans (Thompson and Willson 1979), ants (McDiarmid et al. 1977; Thompson and Willson 1978; Howe 1980; Herrera and Jordano 1981), and rot (Kear 1968; Della-Bianca 1979) have been mentioned as predispersal damaging agents for a variety of wild ripe fruits in tropical and temperate regions. Based on my field experience, I have compiled a crude list of agents damaging to ripe fruits of Spanish plants (table 1).

The most obvious negative effect to the parent plant as a result of damage to fruit flesh is a possible reduction in the viability of the enclosed seeds (e.g., Janzen 1971; Christensen 1972; Pugh 1973; Catalán 1978). On the other hand, damage to the pulp by invertebrates may open the way to subsequent attack by pathogens. The latter not only will eventually destroy any remaining pulp, but also probably will make the fruit objectionable to dispersers from the early stages of infection through the production of toxins or other discouraging substances (Mirocha and Christensen 1974; Janzen 1977*b*). I do not know of any study demonstrating refusal of damaged fleshy fruits by dispersal agents (but see Salomonson and Balda [1977] and Gilbert [1980] for supporting evidence), although equivalent discriminative capacities have been documented for some seed-eating vertebrates (Ligon and Martin 1974; Sork and Boucher 1977; Bossema 1979). It is reasonable to assume that any impairment in the attractiveness of the part of the fruit designed to play precisely an attractive role will result in a decrease of the chance

TABLE 1

NONVERTEBRATE DAMAGING AGENTS TO RIPE FRUITS OF VERTEBRATE-DISPERSED PLANTS IN SOUTHERN SPAIN

Plant Species	Damaging Agent	Part of Fruit Attacked
Berberis hispanica (Berberidaceae)	*Ephippigerida zapatari* (Orthoptera:Tettigoniidae)	flesh and seeds
Crataegus monogyna (Rosaceae)	rot	whole fruit
Daphne gnidium (Thymaelaeaceae)	Unident. Hemipteran; Unident. Orthopteran	flesh and seeds
Daphne laureola (Thymaelaeaceae)	*Dolycoris baccarum, Carpocoris fuscispinus* (Hemiptera:Pentatomidae)	flesh (and seeds?)
Ficus carica (Moraceae)	Unident. Coccidae and fly larvae	flesh (and seeds?)
Iris foetidissima (Iridaceae)	rot	flesh (aril)
Juniperus communis (Cupressaceae)	Lepidopteran larvae	flesh (and seeds?)
Juniperus thurifera (Cupressaceae)	Unident. Coccidae and Lepidopteran larvae	flesh and seeds
Lonicera implexa (Caprifoliaceae)	Unident. pathogen	whole fruit
Olea europaea var. *sylvestris* (Oleaceae)	fly larvae; *Crematogaster scutellaris* (Hymenoptera: Formicidae)	flesh
Osyris quadripartita (Santalaceae)	*Aphaenogaster senilis, Formica* sp. (Hymenoptera: Formicidae); *Sehirus melanopterus* (Hemiptera:Cydnidae); rot; Microlepidopteran larvae	flesh
Paeonia broteroi (Paeoniaceae)	*Ephippigerida zapatari, Antaxius kraussi* (Orthoptera:Tettigoniidae)	flesh (aril) and seeds
Rhamnus alaternus (Rhamnaceae)	*Gonocerus insidiator* (Hemiptera:Coreidae)	flesh (and seeds?)
Rhamnus lycioides (Rhamnaceae)	*G. insidiator; Lygaeus saxatilis* (Hemiptera:Lygaeidae); Unident. Aphidae	flesh (and seeds?)
Rhus coriaria (Anacardiaceae)	rot	whole fruit
Rosa canina (Rosaceae)	rot	whole fruit
Rubus ulmifolius (Rosaceae)	*Carpocoris fuscispinus, Holcostethus vernalis* (Hemiptera: Pentatomidae); *Coreus marginalis* (Hemiptera: Coreidae); rot	flesh (and seeds?)
Sambucus nigra (Caprifoliaceae)	*Holcostethus vernalis* (Hemiptera:Pentatomidae)	flesh
Tamus communis (Dioscoreaceae)	rot	whole fruit

NOTE.—All cases refer to fruits attacked while still attached to the parent plant. Instances of fruits decaying after falling to the ground and injuries to unripe fruits have been excluded.

TABLE 2

SEASONAL VARIATION IN THE INCIDENCE OF DAMAGE TO RIPE FRUITS OF SOUTHERN SPANISH VERTEBRATE-DISPERSED PLANTS

	SPECIES WITH RIPE FRUITS AVAILABLE	INCIDENCE OF DAMAGE (% species affected)		
		by Insects	by Pathogens	Total
January-February	24	8.3	16.7	25.0
March-April	10	10.0	20.0	30.0
May-June	8	25.0	25.0	50.0
July-August	25	40.0	0	40.0
September-October	43	14.0	4.6	18.6
November-December	33	3.0	9.1	12.1

NOTE.—Mainly based on data from 6 study localities and 64 plant species (Herrera 1982, unpubl.). Details of injuring agents and plant species affected are shown in table 1.

of seed dispersal. Ample discussion on this aspect is provided by Janzen (1977*b*) and it may readily be deduced from his reasoning that the pathogen-disperser battle has two losers, disperser and plant, when the pathogen is the winner. Hence we must expect natural selection to have strongly favored those genotypes whose ripe fruits are relatively better protected from irreversible damage.

POTENTIAL MECHANISMS OF FRUIT DEFENSE

Ripening fruits when pest pressure is lowest.—This alternative is favored especially in seasonal habitats where invertebrate abundance and/or environmental conditions conducive to the growth of pathogens fluctuate in the course of the year. Thompson and Willson (1978, 1979) showed that ripe fruits in the field were most frequently attacked by invertebrates in early and midsummer, and suggested that the persistence of undamaged ripe fruits throughout the winter was made possible by the scarcity of injuring agents during that period (see also Snow 1971; Sherburne 1972; Stiles 1980).

Seasonal variation in the incidence of fruit damage is evident among southern Spanish vertebrate-dispersed plants (table 2). Instances of invertebrate damage are proportionally more frequent in spring and summer, which indicates that the risk of fruit destruction is highest when invertebrates are most abundant. On the other hand, fruit attack by pathogens is most severe during the second half of the mediterranean rainy season when ambient humidity and warm temperatures favor the growth of these organisms. The period of the year when most plant species bear ripe fruits (September-December) is that showing the lowest overall incidence of damage.

Reducing exposure time of ripe fruits to noxious agents.—All else being equal, the probability of a ripe fruit being found by phytophagous insects or infected with fungal spores will monotonically increase with length of exposure time; this effect has been clearly demonstrated by Thompson and Willson (1978).

Persistence time of ripe fruits may only be partially and/or indirectly controlled by the plant. Factors such as potential disperser abundance, attractiveness of fruits to dispersers, and competition among simultaneously fruiting plants for disperser services, are some variables interacting intricately to make difficult a fine-tuned control of persistence time of ripe fruits by the plant (Sherburne 1972; Stiles 1980). The only thing plants can do in this respect is to modify ripening rates, and hence the mean persistence time of individual ripe fruits. Modification of ripening rates seems to represent a successful means of escape from damaging agents in habitats with seasonally varying pest pressure (Thompson and Willson 1979).

Fruits may benefit from a decrease in the risk of damage with respect to other plant parts. For phytophagous insects, bacteria, or yeasts, mature fruits are not safe places to live, for they characteristically advertise themselves and become a target for feeding vertebrates. This makes fruits relatively unprofitable objects of specialization over evolutionary time. The relative safety of a mature fruit to a pest will increase as the probability per time unit of the fruit's being consumed decreases. All else being equal, this implies that the longer the average time between ripening and dispersal, the more likely the "colonization" of ripe fruits by pests over evolutionary time (Janzen 1968). Therefore in addition to the previously mentioned short-term, nonevolutionary effects of ripening-to-consumption times on damage risk, persistence time after ripening also negatively influences fruit success by providing ecological opportunities for the evolution of nonvertebrate frugivory. This argument refers, obviously, only to unspecialized pests lacking defensive adaptations against frugivore consumption (Janzen 1977*b*).

Reducing nutritive profitability of fruits.—Invertebrates and pathogens typically spend most or all of their lives in a restricted feeding environment. If fruit flesh does not provide a balanced and sufficiently rich ration, it may not be worth specializing on it or including it in the array of potentially usable foods. Reducing the nutritive profitability of fruit flesh may thus be an alternative defense for plants and may be achieved by decreasing the nutritive content of the flesh and/or by adding chemical or mechanical defenses to the flesh, rendering nutrients and calories difficult for the pest to harvest (Feeny 1975).

a) Providing an unbalanced and/or poor ration. This represents a passive, inexpensive defense. The pulp of most fruits is not very nutritious, and virtually all fruits display an unbalanced combination of nutrients. Although considerable variation occurs (White 1974; Herrera 1981*a*, 1982), fruit pulp is typically high in water and carbohydrates, low to medium in lipids, and extremely low in protein (Hulme 1970; Snow 1971; White 1974; Herrera 1982). Reported variation is always related to the caloric component, particularly lipids, and never to the protein content, which remains within narrow limits and at very low absolute values. Protein content of pulp oscillates between 1.3%–24.5% dry weight (average ± SE = 6.8 ± 0.4%; 124 tropical and nontropical species; White 1974; Herrera 1982, unpubl.).

Nitrogen content is perhaps the most limiting factor in diet selection by herbivores (e.g., Onuf 1978; Milton 1979; Mattson 1980; McClure 1980). Although the origin of nitrogen scarcity in fruits is probably more related to nutrient budget limitations than to a defensive necessity, the consistent nitrogen deficiency of fruits, which places them among the poorest protein sources in nature (see e.g., Mattson 1980), may often be a proximate cause of pests finding them relatively unsuitable as food, particularly during their developing, nitrogen-demanding stages (Slansky and Feeny 1977; Auerbach and Strong 1981; Scriber and Slansky 1981).

Nutritional imbalances of fruit pulp may be, and often are, related to components other than nitrogen such as water, carotenes, organic acids, vitamins, and minerals. These substances often reach very high concentrations in fruit pulp (e.g., Kuusi 1969; Ulrich 1970; Goodwin and Goad 1970; Centenaro et al. 1977; Pulliainen 1978), thus providing the basis for a similar passive defense method based on the presentation of an extremely unbalanced food.

b) Achieving some degree of constitutive resistance.—This represents an active, expensive defense method. This option would imply either mechanical (hard exocarps, resistant skins) or chemical defenses. I wish to stress the latter, which could be accomplished by the placement in the flesh of substances acting as poisons, feeding deterrents, or growth inhibitors of fruit pests. Regardless of whether they met primary or secondary functions in plants (Seigler and Price 1976; Jones 1979), and despite some apparent exceptions (Fox and Macauley 1977; Balick et al. 1978; Bernays 1978; Morrow and Fox 1980), by now it is remarkably well established that secondary compounds found in plants play an important role in the defense against pathogens and herbivores (e.g., Feeny 1970; Whittaker 1970; Whittaker and Feeny 1971; Levin 1971, 1976; McKey 1974; Feeny 1976; Swain 1977; Rosenthal and Janzen 1979).

Whereas chemical defenses in immature fruits fit logical expectations, elimination of these substances during ripening has been considered a necessity which has found support from abundant evidence (e.g., McKey 1974, 1975, 1979; Sherburne 1972). McKey (1974, 1979) pointed out that chemical defenses allocated to immature fruit should be neutralized upon maturation so that the fruit is attractive to dispersal agents. Nevertheless, as shown below, ripe fruits often contain a variety of secondary compounds, thus suggesting that the fruits of many plants represent compromise solutions to the defense-attraction functional conflict.

The main "families" of plant secondary compounds (Harborne 1977; Rosenthal and Janzen 1979) will be shown to be present in the pulp of mature vertebrate-dispersed fruits. Reviews dealing with the significance of these substances have recently appeared (e.g., Cruickshank and Perrin 1964; Levin 1976; Harborne 1977; Rosenthal and Janzen 1979; Friend 1979; Swain 1979*a*) indicating that the substances enumerated in the following sections are all known to be biologically active against pathogens and invertebrates. This also applies to the simplest phenolics such as cinnamic acid derivatives and anthocyanins (Masquelier 1959; Cruickshank and Perrin 1964; Fawcett and Spencer 1969; Swain 1979*a*).

SECONDARY COMPOUNDS IN THE FLESH OF RIPE FRUITS

Following what seems to be a rough natural division of secondary compounds (Feeny 1976; Rhoades and Cates 1976; Maiorana 1979), I will separate secondary substances found in ripe fruits into toxins and quantitative defenses, while recognizing that this may often be more of a matter of convenience than a real dichotomy.

Toxins

To start, I would warn the reader not to think of edible table fruits, which have largely become artificial products after centuries of selective breeding for desirable qualities. Vegetable food used by man represents a strongly biased subsample of nature (Feeny 1977), and one likely criterion used by early man to consider a fruit species susceptible to cultivation could easily have been the absence of toxic substances in the fresh pulp.

Even though McKey (1974, 1979) stated that the disappearance of defensive compounds, particularly alkaloids, from mature animal-dispersed fruits is well known in the Solanaceae, the ripe berries of some European *Solanum* species are reputedly poisonous to man (e.g., Dewberry 1950; Polunin 1974; Catalán 1978; Altmann 1980). If alkaloids are actually involved in that poisoning, this suggests that they experience a reduction in concentration rather than a complete degradation. On the other hand, important concentrations of alkaloids have been reported in mature berries of other Solanaceous species in the genera *Solanum, Mandragora*, and *Atropa* (Kammathy et al. 1974; Jacob et al. 1975; Coune and Denoel 1975; Phillipson and Handa 1975, 1976; Font Quer 1980). This suggests that degradation of alkaloids in wild species of the Solanaceae upon fruit maturation may be only partial at best. Alkaloids have also been reported from the fruits of species in other plant families, such as some Menispermaceae and Celastraceae (Budzikiewicz et al. 1972; Elsohly et al. 1976; Wilkinson 1978).

In addition to alkaloids, an enormous variety of potentially poisonous substances are known to occur in the pulp of wild ripe fruits of many plant families. These include, among others, saponins, cucurbitacins, nonprotein amino acids, steroids, and terpenoids (e.g., Hegnauer 1964; Yang and Mickelsen 1969; Fawcett and Spencer 1969; Goodwin and Goad 1970; Khan and Zehra 1975; Aoki et al. 1976; Seifert et al. 1976; Schauenberg and Paris 1977; Morley 1978; Janzen 1978; Mabry and Gill 1979; Rosenthal and Bell 1979; Altmann 1980; Budzikiewicz and Thomas 1980; Font Quer 1980; Thomas and Budzikiewicz 1980*a*, 1980*b*).

Patterns of occurrence of "toxic" fruits in European plants.—Contrary to expectations as to how should they be, fruits from a variety of plant families may actually contain poisonous substances in the flesh. Two questions are relevant at this point: How widespread are toxic fruits in a regional or continental flora? Does their occurrence exhibit some pattern?

Toxicity is not an inherent property to any substance or chemical structure. A given compound may be a poison to some organisms while being tolerated by others (Janzen 1978; Fink and Brower 1981). Nevertheless, the existence of many plant species whose fruits are toxic to man suggests the presence of biologically active substances which might serve defensive purposes in the fruit. Among 72 plant genera native to Europe which produce fleshy fruits adapated for vertebrate dispersal (after Polunin 1974), 25 genera have been reported as having some species with fruits edible to man, 26 genera are explicitly reported as containing

TABLE 3

DISTRIBUTION OF EUROPEAN FRUIT-PRODUCING PLANT GENERA ACCORDING TO GROWTH HABIT AND EDIBILITY BY MAN*

	NUMBER OF PLANT GENERA (% by rows)		
GROWTH FORM	Edible	Toxic	No Data
Herbs	2 (8.9)	15.5 (68.9)**	5 (22.2)
Shrubs and woody vines	12.5 (33.3)**	10 (26.7)	15 (40.0)
Trees	10 (83.3)	0 (0)	2 (16.7)
Total	24.5 (34.0)	25.5 (35.4)	22 (30.6)

* Based on information in Dewberry (1950), Ceballos and Ruiz (1971), Polunin (1974), Altmann (1980) and Font Quer (1980).

** Species of *Sambucus* (Caprifoliaceae) are reported as either toxic (*S. ebulus*, a herb) or edible (*S. nigra*), thus this genus has been split into two classes.

some species with fruits toxic to man, and no formal statement in any sense was found with regard to species in 22 genera (table 3).

A clear pattern emerges when European fruit-producing plants are classed according to growth form and fruit edibility to humans (table 3). Toxic fruits are strongly overrepresented among herbaceous genera and absent among trees. Overall, the pattern is highly significant ($G = 29.4$, df = 4, $P \ll .001$), demonstrating an actual association between growth form and fruit edibility. Sixty-nine percent of herbaceous genera produce toxic fruits, while corresponding figures for shrubs-plus-vines and trees are 27% and 0%, respectively. For edible fruits, the pattern is reversed, with 9%, 33%, and 83% of herbaceous, shrubby, and arboreal genera, respectively, containing edible fruits.

When edible and toxic fruit-producing genera are fused into a single sample, the frequency distribution of growth forms does not differ statistically from that found in the "no data" group ($G = 3.5$, df = 2, $P = .17$), suggesting that this latter group tends to have a random basis and that further instances of toxic fruits should be expected within that group. It may conservatively be estimated that about one third of European fruit-producing plant genera have fruits toxic to man and these are mostly herbaceous forms.

Quantitative Defenses

In addition to poisons, other secondary compounds designated "quantitative defenses" (Feeny 1976) are found in fruits. Resins, gums, or volatile oils have been reported from the fruit pulp of wild species in the families Anacardiaceae, Lauraceae, Cupressaceae, and Leguminosae (Heim de Balsac 1935; Hegnauer 1962, 1964, 1966; Fahn and Werker 1972). Nevertheless, phenolics are, by far and large, the most widespread secondary compounds in ripe fruits. Common phenolics include cinnamic acid derivatives, flavonoids, and condensed polyphenols (Van Buren 1970). Chlorogenic acid and some of its isomers are common in fruits (Harborne 1964), and anthocyanins are prominent components of the phenolic fraction of fruits (Harborne 1964; Harborne and Simmonds 1964; Van Buren 1970; Lowry 1976). Flavonol glycosides and condensed polyphenols are also normal constituents of ripe fruits (e.g., Vázquez 1965; Vázquez et al. 1974; Liu and Ogihara 1975). In addition to being quite diverse, phenolics are also abundant in ripe fruits and quantitative analyses have most often revealed important concentrations (e.g., Wainio and Forbes 1941; Hegnauer 1966; Van Buren 1970; Vázquez et al. 1971; Gartlan et al. 1980).

From the literature on cultivated plants (e.g., Van Buren 1970), one could get the impression that compounds of smaller molecular weight are the only significant phenolics in ripe fruits, while medium-to-large-sized molecules possessing the astringent reaction of tannins (Bate-Smith 1973; Swain 1979*a*, 1979*b*) are lost upon maturation by increasing polymerization into much larger, nonastringent molecules (Goldstein and Swain 1963; Van Buren 1970; McKey 1979). Nevertheless, tannins are often found in wild ripe fruits (Gartlan et al. 1980; Howe and Vande Kerckhove 1981). Astringency, the best evidence for the presence of typical tannins (Bate-Smith 1973; Swain 1979*a*, 1979*b*), is a conspicuous feature of the ripe fruits of many wild species (see e.g., Ceballos and Ruiz 1971; Polunin 1974; for European species).

CHEMICAL FRUIT DEFENSES AND FRUGIVORE FEEDING BEHAVIOR

Secondary compounds found in fruits do not differ substantially from those in other plant parts, and thus the nature of their effects on vertebrate consumers must presumably be roughly similar. It appears reasonable to predict that if frugivores respond to toxins and digestion inhibitors in fruits in a similar manner as generalized herbivores do when they feed on other plant parts (see e.g., Freeland and Janzen 1974; Fitzgerald 1978; Milton 1979; Oates et al. 1980; Waterman et al. 1980), then the most obvious short-term effect of chemical defenses in fruits will be some depression in the consumption of fruits by individual dispersers and/or a decrease of their actual food value, and thus presumably a decrease in fruit attractiveness. Consequently, some competitive disadvantage may be expected for species and/or phenotypes producing chemically defended fruits.

Although this circumstance seems to have been overlooked by most authors, there is substantial evidence in the literature of infrequent consumption of toxic fruits by dispersers. In North America, Sherburne (1972) found that the fruits of *Ligustrum vulgare* (Oleaceae) and *Viburnum opulus* (Caprifoliaceae), which are toxic to man (Kear 1968; Polunin 1974), were avoided by all birds, remaining virtually uneaten while other coexisting plant crops were being totally exhausted. Avoidance of *V. opulus* by birds was also mentioned by Docters van Leeuwen (1954, p. 177). Kear (1968) reported that most fruit crops of several British species having toxic fruits usually remain uneaten on the plant. I have similarly failed to find any reference to birds or mammals actually feeding on other European toxic fruits (e.g., *Mandragora, Arum, Calla*), despite exhaustive reviews of frugivory (Ridley 1930; Schuster 1930; Turcek 1961, 1967). There are, however, records of birds feeding occasionally on some other European toxic fruits, suggesting the existence of a continuum of toxicity-mediated acceptability (see table 4).

Differential consumption by avian frugivores of fruit species unrelated to variation in caloric reward, abundance, or searching/handling efficiency has been reported by Sherburne (1972) and Sorensen (1981). The latter author suggested that palatability and/or the presence of secondary compounds in the fruits could serve to explain these patterns. Active avoidance of toxins by avian frugivores has been experimentally demonstrated by Sherburne (1972).

The influence of quantitative defenses on food selection by frugivores is difficult to detect in general studies as those quoted above and I did not find references to document these effects. Nonastringent phenolics almost universal in fruits such as anthocyanins and highly condensed polyphenols probably will not have any detrimental effect on frugivores. Tannins present in astringent ripe fruits almost certainly will have some digestive inhibitory activity (Feeny 1969; Perrins 1976; Swain 1979*a*, 1979*b*) and, all else being equal, they will probably give some competitive disadvantage to fruits.

Chemical fruit defenses and "filtering out" of dispersal agents.—Spatio-temporal patterns of fruit presentation, size and nutritional value of fruits, and crop sizes, among others, have been related to disperser selection by plants to obtain the best prospects for dispersed seeds (Snow 1971; McKey 1975; Howe 1977; Howe and Estabrook 1977; Howe and Vande Kerckhove 1979; Howe 1979, 1980). Although secondary compounds in ripe fruits probably have their ultimate origin in a defensive necessity, these substances may have played other secondary roles in shaping plant-disperser interactions. Janzen (1978, 1979*b*) suggested that toxic chemicals in fruits could serve to filter out dispersal agents by excluding undesirable dispersers which do not tolerate the toxins in the fruits. Similarly, he interpreted the broad variety of dispersers visiting *Ficus* trees as a result, in part, of the absence of secondary compounds in their fruits (Janzen 1979*a*). These suggestions have remained untested to date and are relevant here because toxic fruits may be relatively common in some regions.

Among European fruit-producing plant genera, the average number of bird and mammal species per plant genus eating the fruits is significantly lower for toxic than for edible genera (table 4). Proportional depression of consumer diversity by fruit toxicity appears to be slightly larger among mammals (81% reduction, as compared with 61% among birds), although it has roughly the same order of magnitude for both groups. This indicates that toxicity is actually associated with a reduction in the number of species attracted to the fruits, although the data might also be considered indicative of greater rarity or more restricted distributions of toxic-fruit genera (Herrera, unpubl.). A combination of both effects appears most likely.

To determine whether fruit toxicity could exclude differentially some frugivorous groups, I separated all European fruit-producing genera according to fruit edibility and actual consumption by birds and mammals on the basis of the lists published by Turcek (1961, 1967; present study, table 5). A three-way test of independence reveals a highly significant overall relationship among edibility and

TABLE 4

SPECIES DIVERSITY OF FRUGIVORE ASSEMBLAGES FEEDING ON EUROPEAN VERTEBRATE-DISPERSED FRUITS*

	NO. OF SPECIES EATING FRUITS PER PLANT GENUS**	
	Birds	Mammals
Toxic genera (N = 26)***	8.5 ± 10.9	1.5 ± 2.9
Edible genera (N = 25)***	21.8 ± 19.2	8.1 ± 10.1
F-value	9.47	10.20
$P<$	.005	.005

* Based on information in Turcek (1961, 1967). Fruit edibility after references in table 3.

** Mean ± 1 SD.

*** The genus *Sambucus* has been counted twice, *S. ebulus* and *S. nigra* treated separately (see table 3).

bird and mammal consumption. The three pairwise comparisons are also significant, indicating that (1) plant genera producing nontoxic fruits tend to be consumed by both birds and mammals more frequently than expected, and (2) there is an almost complete agreement in the patterns of fruit consumption by birds and mammals, both groups tending to ingest and reject the same fruits.

Data in Turcek (1961, 1967) on which tables 4 and 5 are based do not allow separation of legitimate dispersers from vertebrate frugivores damaging the seeds,

TABLE 5

CONSUMPTION OF TOXIC AND EDIBLE EUROPEAN FRUITS BY BIRDS AND MAMMALS

Edibility (E)	Consumption by Birds (B)	Consumption by Mammals (M)	
		Eaten	Not eaten
Edible	eaten	17	3
	not eaten	1	4
Toxic	eaten	9	3
	not eaten	0	14

NOTE.—Figures represent the number of plant genera falling in each category. Based on data in Turcek (1961, 1967) and references in table 3.

Three-way test of independence:

Hypothesis	df	G-value	P
B × M independence	1	31.80	<.001
B × E independence	1	6.44	<.05
M × E independence	1	7.34	<.01
M × B × E interaction*	1	−4.03	. . .
M × B × E independence	4	41.56	<.001

* Residual G for interaction may be negative because of nonorthogonality of independent binary tests (Sokal and Rohlf 1969, p. 606).

although I am confident that most avian, and a significant fraction of mammalian, species involved do not damage seeds. Data come from inhomogeneous sampling of a broad area and most likely embody an undetermined amount of sampling biases and deficiencies. Keeping in mind these limitations, the data presented serve at least to suggest that fruit toxicity (judged in relation to man) is actually associated with a strong reduction in the size of the feeding assemblages, and that birds and mammals appear to respond similarly to fruit toxicity despite their taxonomic unrelatedness. To demonstrate an adaptive value of fruit toxicity to plants with regard to disperser selection, it is not only necessary to demonstrate a reduction of disperser assemblage, but also to show that excluded species have some characteristics undesirable to the plant (Rhoades 1979). Data presented here are inconclusive in this respect.

DISCUSSION

If, as the above data suggest, chemically defended fruits are at an actual competitive disadvantage relative to nontoxic ones, why then did they evolve at all? Why have they not been outcompeted? Which factors contribute to sustained coexistence? In this section I suggest some possible answers to these questions. Because of the absence of studies bearing on these aspects my approach must remain largely speculative.

Fruits display an astonishing variety in size and structure (van der Pijl 1972). Variation in the within-fruit distribution of secondary compounds, coupled with differences in fruit handling techniques by frugivores, preclude any attempt at broad generalizations. Large fruits adapted for dispersal by vertebrates like mammals possessing manipulative skills might freely accumulate defenses in their outer layer which later could be removed readily by dispersers prior to eating (e.g., citrus, granadillas, large cucurbitaceous fruits). This is not possible for small fruits ingested whole by avian dispersers. For these reasons I prefer to discuss the significance of fruit defenses in relation to a fairly restricted ecological background in which many independent variables (Smith 1975) are held constant. I will concentrate on the relationships between plants and their vertebrate dispersers in a nontropical seasonal habitat, having in mind birds as the dispersal agents.

A Hierarchy of Fruit Defense Methods

The evolution of a particular defense method will depend on the opposing pressures on the plant resulting from the risk of fruit damage and the various costs to the plant from using that defense procedure. Associated costs vary in relation to both plant economics and the effects on disperser feeding behavior (table 6). The most detrimental alternatives involve a decrease in fruit profitability, either by secondary compounds or nutritional insufficiency. These alternatives should be avoided in favor of less expensive ones based on costless temporal escape. I suggest that a "preference" order of defensive methods should exist (1–4 in table 6), and that less advantageous methods should evolutionarily be chosen only if

TABLE 6

GROSS CORRELATES OF THE MAIN FRUIT DEFENSE METHODS

Defense Method	Cost to the Plant in Energy and Nutrients	Effect on Disperser Feeding Response
1. Fruiting during the time of lowest pest pressure	none	variable*, usually positive
2. Reducing exposure time by decreasing ripening rate	none	variable*, often negative
3. Unbalanced and/or poor ration in the flesh	none	negative
4. Chemical defense	some	negative

* Depending on disperser abundance and attractability.

more profitable ones (scoring lower in the ranking of costliness) are precluded or rendered ineffective.

Alternative 1 (table 6) should be the most profitable in all habitats in which the risk of fruit damage changes seasonally. The latter is directly related to pest abundance, but also to fruit persistence after ripening. While pest pressure will be related to season in a fairly straightforward, habitat-specific way (table 2), persistence time simultaneously will depend on disperser abundance, attractiveness of the fruit, and plant competition for disperser services, with all of these variables often co-varying intricately. In temperate habitats, insect abundance fluctuates strongly, with a peak in spring and a low in winter. As a group, insects play three different roles in the plant-bird story. They are pollinators of many plants, food for birds, and damaging agents to fruits; thus their presence may have either beneficial or detrimental effects on both plants and birds. As seasonality in insect abundance increases, there will be greater pressure on plants to separate functions enhanced and impaired by insects so that they coincide with times of high and low insect abundance. On the other hand, attractiveness of fruits to seasonally insectivorous dispersers will vary inversely with insect abundance, being lowest in spring and highest in winter (Morton 1973; Stiles 1980). These convergent pressures on plants will make winter the best time to disperse seeds. Nevertheless, temperate winter is a hard time not just for insects, but also for plants and dispersers, whose physiological activity and abundance, respectively, decrease at that time. These facts, coupled with the increased disperser abundance provided by autumn migrants, have strongly selected for the predominant autumn ripening season characteristic of temperate habitats (Snow 1971; Sherburne 1972; Thompson and Willson 1979; Stiles 1980).

If all plant species in a habitat could successfully ripen their fruits during the best season, further defense methods for the ripe fruit would not be required provided that pest pressure is nonexistent and/or dispersers are superabundant at that time. These conditions are probably never met in nature and further defensive methods should thus evolve. In the next section I hypothesize that (1) unpreferred, detrimental defensive mechanisms will evolve differentially among plant species in a habitat and will be found mainly among competitively inferior species, and (2) pest pressure and plant competition for dispersers are the most likely ultimate causes for some fruits' reliance on unpreferred defensive methods, including chemical deterrents.

Pest Pressure, Plant Competition, and Detrimental Fruit-Defense Methods

Mathematical models of even the simplest plant-animal mutualistic systems present a high degree of formal complexity when the role of nonmutualistic organisms is taken into consideration (Heithaus et al. 1980). The system integrated by plants, dispersers, and fruit pests would be fully described by no less than nine interaction parameters. It is impractical to put forward a general model attempting to depict the complex evolutionary relationships existing between plants, dispersers, and fruit pests and, in particular, the effects of plant competition and fruit predators on the evolution of fruit features. I will present a simple conceptual model to suggest some possible evolutionary pathways leading to chemically defended fruits, based on the assumptions that (1) dispersers discriminate among simultaneously available fruits on the basis of avoiding chemicals, maximizing energy intake, and/or achieving a balanced diet, and (2) the absolute amount of energy and nutrients available to individual plants for the production of fruits has a species-specific upper limit.

Imagine the ideal situation in which all species in a habitat ripen fruits simultaneously during a short time period, when dispersers are most abundant and most attracted to fruits and pest pressure on ripe fruits is lowest. Assume also that all plants share the same dispersers and that some pest pressure on mature fruits does exist at that time. If the fruits of all species are ideal in the sense that they have nothing but disperser-rewarding substances in the pulp in balanced proportions, and dispersers as a whole forage optimally with respect to fruits, then a ranking of feeding preferences will emerge on the basis of the differential reward offered by the various plant species and their relative abundances (Emlen 1966; Pyke et al. 1977). Risk of damage to fruits will be directly related to the time spent on the plant after ripening, which in turn depends on the position held by the plant in the ranking of disperser feeding preferences. Preferred species will probably be those having the most rewarding fruits in terms of fat, protein, and carbohydrates obtainable per mass unit of ingested fruit. They will be competitively superior, rapidly attracting as many disperser visits as required to remove the entire crop.

Ripe fruits of species low in disperser preferences will stay longer on the plant and some of them will eventually be lost to pests or remain undispersed. Over evolutionary time, these plants could improve their competitive ability by producing more rewarding fruits. If allowed by the plant's physiological efficiency and energy and nutrient budget, this option will be enhanced by interplant, disperser-mediated competition until a critical upper limit to investment in fruit reward per seed has been reached and a stable position in the ranking achieved.

Among earlier successional species tending to maximize seed output, the upper limit to nonseed (pulp) investment per individual seed is likely to be low (Salisbury 1942; Abrahamson and Gadgil 1973; Gaines et al. 1974; Abrahamson 1979), and their final position in the competitive ranking will probably be low. On the other hand, the strength of selective forces against fruit destruction presumably must be greatest among these short-lived plants for which the destruction of a single fruit crop is probably more detrimental to the perpetuation of parental genotypes than for long-lived, later successional species with many reproductive episodes during their lifetimes.

A defensive option available to species unable to produce competitive, high-reward fruits could be the modification of ripening rates leading to greater within-crop asynchrony. If crop size remains unaltered, this would lead to spreading the fruiting season beyond the limits of the best safe season. If fruit destruction rates continue to be higher than dispersal rates a supplementary defense mechanism could be to impair the nutritive value of fruits (table 6) to pests without decreasing their attractiveness to dispersers. This may be accomplished by shifting from the ranking of "hard," balanced food to a different one, namely that of accessory, but indispensable nutrients (minerals, vitamins, etc.). These substances are valuable to animals not for their quantity, but rather for specific properties of their molecules, thus they may be termed "qualitative" rewards, as opposed to "quantitative" ones such as fat or carbohydrates whose value increases linearly with the amount ingested. Because they cannot constitute the staple food for any organism, this confers a relative protection from pests. In terms of their synthesizing costs, qualitative rewards are particularly well suited to plants having severe limitations on the nonseed investment per seed.

Still, plant competition may negatively affect the dispersal of some species with qualitative-reward fruits, generating a further necessity of fruit defense among competitively inferior species. Some chemical-defense mechanism could then be favored to avoid premature destruction of ripe fruits by pests and to increase exposure time to dispersers. This option would theoretically take the status of the plant still lower in the ranking and fruits would persist longer, generating a need for further defenses and closing a positive feedback leading to extinction. Nevertheless, the process will not progress indefinitely. Among chemical defenses, qualitative ones (toxins) are incompatible with quantitative-reward fruits which are to be ingested in large amounts by dispersers to get substantial quantities of the massively required calories and protein, but are compatible with qualitative-reward fruits. Because individual dispersers will consume these fruits sporadically, toxins will not accumulate in the gut above critical levels, and probably will not affect the intrinsically low individual consumption rates inherent to this kind of fruit. On the other hand, abundance and crop size will also affect the success of chemically defended fruits. For abundant plants and/or those producing medium to large crops, the "continuous sampling" program (Freeland and Janzen 1974) which individual frugivores presumably follow and which leads them occasionally to ingest unripe fruits (Diesselhorst 1972; Sherburne 1972), will result in the removal of a few fruits, but individual dispersers will not repeat feeding frequently after an initially unrewarding and/or unpleasant experience. For plants having small crops and/or low population density, the low removal rates originated by the food sampling of frugivores nevertheless would remove a sufficient number of fruits to maintain small population sizes. In some sense, these plants would behave much in the same manner as deceptive mimetic fruits do, which provide no reward and whose success depends on their rarity and external resemblance to true, rewarding fruits (Wiens 1978).

Among other limitations, the preceding model only considers the case of fruits defended by toxins and largely ignores the evolutionary potential existing for staggering fruiting times along the seasonal gradient of competition-predation balance. Similarly, it does not incorporate the possible counteradaptations that fruit-defensive traits may select for among dispersers. Despite these limitations, several testable predictions may be suggested which could serve to assess the role played by plant competition, disperser availability, and pest pressure in the evolution of toxic fruits in temperate habitats.

1. In regional vertebrate-dispersed floras there should always exist the entire gradient of "quantitative-reward," "qualitative-reward nontoxic," and "qualitative-reward toxic" fruit types, and these should roughly be associated with arboreal, shrubby, and herbaceous growth forms, respectively. In interregional comparisons, frequency of undesirable fruits should be higher when the abundance of dispersers and/or their competence in finding fruit sources is lower.
2. In habitats with marked fruiting seasonality, chemically defended fruits should be proportionally underrepresented during the peak of fruiting and overrepresented at other times.
3. The most toxic fruits should most often be found among species producing small fruit crops and/or having small population sizes or patchy distributions.
4. Qualitative-reward nontoxic fruits generally should be produced by plants having larger crop sizes than those producing qualitative-reward toxic fruits.
5. Species with toxic fruits that rely on continuous sampling by dispersers for seed dispersal will tend to have a larger number of seeds per fruit than similar species producing nontoxic fruits.
6. In general, chemically defended fruits should possess lower nutritive reward than undefended ones (measured in terms of quantitative substances), and/or provide a more unbalanced food in the flesh. There should be an inverse relationship between mineral, vitamin, and/or other qualitative nutrient content, and fat or protein.

Some of these predictions (1, 3) are partially supported by data presented earlier in this paper (see also Janzen 1977*a*, p. 718), while others must be tested in future studies.

CONCLUSION

The understanding of some features of seed dispersal systems requires a broad approach in which the system is not considered in isolation from external selective pressures. In particular, avoidance of fruit destruction appears to have played a significant role in shaping plant traits related to seed dispersal. Implications of fruit defense certainly go much farther than outlined in this paper. The virtual absence of studies bearing on frugivore food selection, ecological correlates of fruit defense methods, and between- and within-habitat patterns of occurrence of secondary compounds in fruits, have combined to preclude any attempt at completeness. Thus the present contribution is no more than a preliminary exploration of the subject, aimed at illustrating its potential significance and suggesting directions for future studies rather than providing conclusive evidence. Some general insights, however, may be inferred from the information presented.

Had plants and dispersers been living in an ecological vacuum, interacting only with each other, fruits should eventually become ideal, paradigmatic structures, since selective pressures continuously placed on plants by dispersers would select for desirable qualities only. Ideal plant-disperser systems should steadily progress toward situations of close interdependence by means of fine-tuned reciprocal adjustments (coevolution; Janzen 1980). These systems would behave in much the same manner as usual mathematical models of mutualism, which consider the reciprocal interaction between mutualistic organisms in isolation and lead to unrealistic predictions of instability (May 1975; Heithaus et al. 1980). Cultivated fruits illustrate this point. By putting money, effort, and synthetic chemicals into the man-orchard system to eliminate pests, and by ripening fruits in controlled chambers to further reduce risk of damage, man continuously attempts to create an ecological vacuum around his interaction with fruits. Under these conditions, fruits having only desirable qualities (thick pericarp, absence of toxic or unpleasant compounds and, often, seedlessness) have ''evolved'' which probably are ''ideal'' in most respects for the average human frugivore.

In the real world, selective pressures external to the mutualistic system must have served, among other factors (Howe 1980, 1981; Wheelwright and Orians 1982), as a permanent brake to the development of close plant-disperser coevolution as a general, community-wide phenomenon. This apparently has been brought about by the evolution of fruit features undesirable to dispersers as a result of the combined action of fruit predation risk and plant competition for dispersers. Drawing a further analogy with mathematical models of mutualism, this situation would lie close to the ant-myrmecochorous plant system described by Heithaus et al. (1980), whose stability is greatly increased after incorporating into the model the effects of seed predation and plant competition.

The adoption by some plants of fruit-defense methods which secondarily impair attractiveness to dispersers may have facilitated the regional coexistence of many plant species sharing the same dispersers. Varied diets exhibited by all vertebrate frugivores (e.g., Hartley 1954; Snow 1962*a*, 1962*b*, 1962*c*; Bonaccorso 1979; Sorensen 1981; Herrera 1981*b*; Jordano and Herrera 1981), including the most ''specialized'' ones (Wheelwright and Orians 1982), are most likely the outcome of fruits representing poor, unbalanced food items often containing secondary compounds, just the same reasons for which generalized vertebrate herbivores consistently feed on a broad array of vegetable sources (e.g., Freeland and Janzen 1974; Montgomery 1978; Westoby 1978; Milton 1979). Faced with ideal fruits (balanced, nontoxic food) evolved in a predation-free, noncompetitive environment, frugivores' food selection probably would be determined by conventional optimal foraging criteria (e.g., Emlen 1966; Charnov 1973; Pyke et al. 1977) rather than by optimizing diet composition with regard to nutrients and secondary compounds (Westoby 1974, 1978; Pulliam 1975; Milton 1979). In the former situation, plant-disperser coevolution could progress among competitively superior plant species, but at the expense of inferior competitors being eliminated from the scene as a result of the absence of ''partial food preferences'' by frugivores (Pulliam 1975; Westoby 1978). Increased opportunities for plant coexistence provided by fruit modifications related to competition and predation are conceptually equivalent to the increased coexistence potential provided by the staggering of fruiting and flowering seasons in response to plant competition for dispersers (Snow 1965; Smythe 1970) and pollinators (Mosquin 1971; Stiles 1975, 1977; Heinrich 1976). In the case of relatively undesirable fruits, we arrive at the paradox of competition being ultimately responsible for the appearance of proximate mutualistic interactions between plant species (see e.g., Waser and Real 1979).

SUMMARY

Ripe fruits of vertebrate-dispersed plants are susceptible to irreversible damage by pathogens and invertebrates while they are attached to the parent plant "waiting" for the visit of a dispersal agent. Adaptations of plants to decreasing fruit damage include temporal escape from pests, reducing exposure time, and decreasing fruit profitability to pests by means of secondary compounds and reduced and/or unbalanced nutrient content. A variety of secondary compounds has been reported from the ripe fruits of many vertebrate-dispersed plants, including alkaloids, saponins, volatile oils, resins and phenolics. Toxic fruits containing poisonous substances that potentially are defensive agents against pests may be very frequent, as revealed by an analysis of their occurrence among European plants.

As judged from the literature, fruits containing secondary substances are at a competitive disadvantage relative to nontoxic ones. It is suggested that a hierarchy of fruit defense methods should exist, with the least desirable ones selected for only when better mechanisms are precluded or rendered ineffective. A simplified model is proposed to explain the occurrence of toxic mature fruits; the roles of pest pressure and plant competition for disperser services are considered, and some testable predictions are suggested. It is finally argued that nutritionally unbalanced fruits or those with secondary compounds probably serve indirectly as a means of increasing the potential for plant coexistence through their diversifying effects on diet selection by individual frugivores.

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